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THE ORIGIN OF CORN

I. POD CORN, THE ANCESTRAL FORM

BY

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IT IS now one hundred years since the first edition of Darwin's epoch-making book "On the Origin of Species" appeared in the London bookstalls. It would be difficult to overestimate the immediate impact of this work, or its continuing influence throughout the ensuing century, not only upon all branches of biology but also upon the other sciences and indeed upon virtually all fields of human thought. It has been said with some degree of truth that "Next to the Bible no work has been quite as influential, in virtually every aspect of human thought, as the 'Origin of Species.' "

To the student of cultivated plants, the book was — and is — of special interest because Darwin's conclusions, arguments and theories were founded, to a large extent, on his monumental studies of domestic animals and cultivated plants. The first chapter in the book is devoted to this subject, and Darwin subsequently wrote a two-volume treatise on the variation of animals and plants under domestication. He believed that the key to the problems of modification and adaptation was to be found in the study of variation of organisms under domestica-

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tion. A passage in the introduction to "On the Origin of Species" makes this abundantly clear:

At the commencement of my observations it seemed to me probable that a careful study of domesticated animals and of cultivated plants would offer the best chance of making out this obscure problem. Nor have I been disappointed; in this and in all other perplexing cases I have invariably found that our knowledge, imperfect though it be, of variation under domestication, afforded the best and safest clue. I may venture to express my conviction of the high value of such studies, although they have been very commonly neglected by naturalists.

Darwin's studies on domestic animals and plants, together with those of De Candolle on the origins of cultivated plants, have been the inspiration for our own work, at once more restricted in its scope and more intensive in its treatment, on the origin of Indian corn. It is now twenty years since we proposed the tripartite theory² which postulates (A) that cultivated maize originated from a wild form of pod corn which was once indigenous to the lowlands of South America; (B) that teosinte (*Zea mexicana*), the closest relative of maize, is the product of a natural hybridization of *Zea* and *Tripsacum* which occurred after cultivated maize had been introduced by man into Central America; (C) that new types of corn originating directly or indirectly from this cross and exhibiting admixture with *Tripsacum* or teosinte comprise the majority of modern Central American and North American varieties.

During these twenty years, an impressive volume of new research bearing on the problem has been completed, much of it stimulated and guided by the theory itself.

² In this paper we, like other students of maize, use the word "theory" in its popular or semipopular meaning. In a strict sense, we are not dealing with theories — certainly not with theories involving broad principles — but with hypotheses. Webster's Dictionary defines hypothesis as "a tentative theory or supposition, provisionally adopted to explain certain facts and to guide in the investigation of others."

During this same period, the theory has also been the object of lively controversy and of strong objections. On this hundredth anniversary of the publication of Darwin's "On the Origin of Species" and the twentieth anniversary of our own more modest contribution, it seems appropriate to take a broad new look at the entire problem of the origin of corn — a problem which not only is fascinating in its own right, but one whose solution promises to shed some light on the evolution of other cultivated species. It is our purpose, then, to evaluate both the old and the new evidence as well as the objections; to consider the various theories which have been proposed; and to review the extensive relevant literature which has appeared in the last two decades.

In discussing theories on the origin and evolution of maize, it is perhaps inevitable that we should give major attention to our own. There is nothing unusual in this situation. Most new theories, if they are taken seriously at all, have strong objections raised against them. It is one of the obligations of their authors to give serious consideration to these objections and to answer them if possible, since if they fail to do so, it may erroneously be assumed that the theory has been disproved. If the objections cannot be answered in a logical and plausible way with the facts at hand, then either the theory is weak and requires modification or more evidence is needed. In either case, the free exchange of opinions, although seldom completely objective on either side, can serve a useful purpose. Controversy — up to a point — can sometimes be as useful as research in clarifying a problem.

GENERAL CONSIDERATIONS

Most of the objections to our tripartite theory of the origin of maize are directed specifically at one of its three parts, but some are of a more general nature. These are

considered here: Weatherwax (30) says of the theory: "Its most obvious general weakness is that there is so much theory in proportion to the available facts. It is topheavy with assumptions of such character that if any one of them should be rejected the whole structure would fall." And in essentially the same words he reiterates (31): "Our principal criticism of this ingenious explanation is that it involves too much theory for the facts. It is top-heavy with premises so interdependent that the failure of any one of them will cause the whole structure to fall."

Whether or not the theory is top-heavy with unsupported premises is largely a matter of personal opinion, and each reader is entitled to his own. However, if Weatherwax's statements were once true, they are certainly less so today, for the theory now has much more evidence in its support than when it was first proposed or even when the objections quoted above were made. Furthermore, these objections have overlooked some of the significant evidence which was even then available. We are disturbed by the fact that the extensive bibliography, which is a part of the joint chapter by Weatherwax and Randolph in a recent book (25), omits a number of significant papers. The omissions are especially unfortunate when the authors cite one paper (26) which they believe supports their conclusions and omit two others published in the same journal (21, 33) which are contrary to them.

The statements with regard to the interdependence of our premises and the charge that "if one of them should be rejected, the whole structure would fall" are simply without foundation. It should be obvious, and in an earlier publication (18) we have emphasized the fact, that the three parts of this theory, although providing an integrated picture of the origin of corn, are, to a large ex-

tent, independent of each other. This becomes clear if we invert the argument and ask whether proof of one part of the theory proves the other two as well. For example, would the discovery of a wild or fossil form of pod corn, although clearly proving pod corn to be the ancestral form, either prove or disprove the assumption that teosinte is a hybrid of maize and *Tripsacum* or that modern varieties of maize have been modified by introgression from teosinte? Or would proof that teosinte can be artificially produced by hybridizing maize and *Tripsacum* prove also that pod corn is the ancestral form and that modern corn is strongly contaminated with teosinte?

Since the three parts of the theory are obviously to a large extent independent, it seems appropriate to discuss objections to them separately. The remainder of this paper is concerned only with the first part: the postulate that cultivated corn originated from a form of pod corn. The succeeding papers in this series will treat other aspects of the problem.

POD CORN, THE ANCESTRAL FORM

The theory that cultivated maize originated from pod corn, a form in which the individual kernels are enclosed in floral bracts as they are in other cereals and in the majority of grasses, is not original with us, although we have made a contribution to it by adding the assumption that the ancestral pod corn was necessarily quite different from the monstrous pod corn found in modern, highly domesticated varieties. The original idea we owe to Saint-Hilaire (23), who was apparently the first to offer any comment on the origin of cultivated maize and also the first to suggest that pod corn represents the ancestral form. We adopted the pod-corn theory only after our extensive studies of maize-teosinte hybrids had suggested to us that teosinte is itself a hybrid of maize and

Tripsacum and could therefore be dismissed as the ancestor of corn. Pod corn, then, appeared to be the only plausible alternative to teosinte as the progenitor, unless we resorted, as have several of our critics, to a strictly hypothetical ancestral form which is now extinct.

The strongest objections to the pod-corn theory have come from Weatherwax (29, 30, 31). They fall into seven principal categories: (A) Pod corn is "equivocal," a word of many meanings, which when used in this particular context, seems to be more or less synonymous with "extremely variable." (B) It is monstrous and sterile. (C) It is similar to other monstrosities like teopod and corn grass. (D) It does not have the characteristics of a wild grass. (E) It could not have existed in the wild. (F) It is the product of plant hormone action. (G) The weaker form of pod corn, "half tunicate," which at first glance seems to be a more promising ancestral form, affects only the glumes and does not influence the other characteristics of the plant. Let us examine these objections separately.

(A). The first objection is fallacious in two respects: (a) The character, although often variable, is little, if any, more so than other characteristics of the corn plant, such as monoecism and the ear itself—two features which distinguish corn from all other important cereals. If, in attempting to reconstruct the ancestral form, we are to rule out all characters of the corn plant which are highly variable, we can do little more than say that it was a grass, a fact on which all students of the subject have so far been in remarkable agreement. (b) Pod corn actually is not at all equivocal when the genetic background and environment are held constant. Through repeated back-crossing, we have transferred both the *Tu* and the *tu^h* genes to two inbred strains, A158 and P39. Although the different genotypes which can be produced with the

three alleles at this locus are very different in the two inbreds and their hybrids, there is little if any more variation within the genotype than there is in nontunicate ears of these same inbred strains. The uniformity within any one genotype, when the alleles at the pod-corn locus are incorporated into a uniform genetic background, proves that the variability of pod corn — what has been called its “equivocal” nature — is primarily a matter of variation in the genetic background. What we see in any ear or plant of pod corn is the product not only of the *Tu* or *tu^h* gene but of these genes interacting with all other genes.

(B). The interaction of the tunicate gene with other genes is an important fact to be remembered in considering the second objection, that pod corn is monstrous. This objection is not only beside the point, since we have always assumed that the ancestor of corn was necessarily a non-monstrous form of pod corn, but it is also not valid. It is, of course, true that modern pod corn is often monstrous, especially when homozygous. We believe, however, that its monstrousness has been misunderstood; pod corn is monstrous today only because it is a wild relict character (a conclusion reached also by Brieger, 4, 5, 6, 7) superimposed upon modern, highly heterozygous and vigorous varieties, some of them the product of teosinte introgression. Today's pod corn is comparable to a 1900 chassis powered by the engine of a 1959 car. The surprising thing is not that pod corn is somewhat monstrous but that it is not more so—that the particular genic locus that governs its expression is capable of functioning at all in a milieu so different from that in which it once served and to which it was undoubtedly well adapted. We have assumed that pod corn would be less monstrous and would exhibit normal grass characteristics when combined with the other “wild” genes. Brieger

(5, 6) sought these in corn's relative, teosinte; we hoped to find them in varieties of popcorn. This hope has been realized as will become apparent later in this paper, when the genetic reconstruction of the ancestral form of corn is described.

The sterility of homozygous pod corn, like its generally monstrous nature, has evidently also been misunderstood. Weatherwax mentions its "self-sterility" — an inaccurate term — and states that little, if any, pollen is produced and that this is rarely functional. Brieger (5) states that the sterility is "still unexplained." Actually, sterility is not an inherent characteristic of pod corn; it is, in fact, nothing more than a strictly physiological or mechanical effect of overgrown glumes. If the glumes are monstrous, the anthers do not reach full development; apparently they do not compete successfully for energy with the rampantly-growing glumes. A potentially sterile tassel of homozygous pod corn can sometimes be induced to become fertile by the early removal of the central spike which is usually massive and bears the most monstrous glumes.

If the glumes are well developed but not particularly monstrous, the anthers may develop normally but fail to be exerted. Under these conditions, they may shed their pollen while still enclosed within the glumes. This pollen, which sifts out between the glumes in considerable amounts, is perfectly normal in appearance and is quite functional. We have produced a number of progenies in which all of the plants were of the genotype *Tutu* by collecting such pollen and applying it to the silks of normal plants.

If the glumes are shortened still further by combining the *Tu* gene with appropriate modifiers, then the anthers not only develop normally but are also normally exerted. We now have strains of homozygous pod corn which

regularly exert their anthers and shed pollen abundantly. There is no basis whatever for the suggestion (31) that we have, through selection, imparted fertility to a type of maize which never before possessed it. What we have done is merely to reduce the monstrosity of pod corn by combining the *Tu* gene with modifying and inhibiting genes, so that the glumes of the staminate spikelets no longer interfere with the development or release of the pollen. There is no type of pod corn so monstrous or so sterile that it cannot be changed in a few generations to a normal, fertile type by introducing modifying and inhibiting genes from varieties of popcorn.

(C). The comparison of pod corn to other single-gene anomalies in maize, especially teopod and corn grass, is not as significant as it might at first glance appear. It is true that both of these types exhibit certain characteristics which might be regarded as primitive (28, 24): for example, a freely-branching growth habit and seeds partly or completely enclosed by floral structures. And pod corn does indeed resemble teopod and corn grass in being often monstrous. But pod corn, however equivocal and however monstrous, consistently and invariably has one important characteristic which the majority of cereals have and which wild maize is generally assumed to have had: glumes enclosing the caryopses. Both teopod and corn grass occasionally have long glumes; more frequently, perhaps, they bear long spathes (9, 28). Neither of them consistently has the essential wild characteristic of glume-enclosed seeds as does pod corn.

In an earlier publication (13), it was emphasized that a mutation to pod corn has never been observed in pedigreed cultures, which, in the production of hybrid seed corn, involve large numbers of artificially pollinated plants. Weatherwax has contended that the failure to find mutations to pod corn in pedigreed stock "need not

be the cause of much concern'' (30), since the occurrence of teopod and corn grass is also infrequent. He is in error. The teopod character has appeared repeatedly in commercial hybrids and is recognized in the hybrid seed-corn industry as a recurring mutant. Corn grass has been found at least twice, according to published reports, and probably many additional times. We know that one corn grass mutant was lost by being hoed out by laborers who thought it to be a weed. How often this has occurred there is no way of telling. In contrast, the mutation to pod corn has never been reported under circumstances where contamination could be ruled out. Millions of ears of inbred strains and their first-generation hybrids have now been studied by corn breeders, and no one has yet reported finding pod corn in a single one.

(D). The contention that pod corn does not have the characteristics expected in a wild grass, especially a freely-branching habit, again overlooks the fact that modern pod corn is the product of a single gene superimposed upon highly domesticated varieties most of which are not themselves freely branching. Weatherwax, himself (27), pointed out many years ago that pod corn is not a variety distinct from all others—that pod corn can be classified as a flint, flour, dent, sweet, or popcorn. By the same token, pod corn can become freely branching if the pod-corn gene is combined with the genes of a freely-branching form. This is well illustrated when pod corn is combined with freely-tillering varieties of popcorn (15). It is strikingly illustrated when it is combined with teosinte, an extremely freely-branching plant.

(E). The assertion that pod corn could not have existed in the wild is based, we believe, on the conception of pod corn as a monstrosity. Certainly the pod corn resulting from incorporating the *Tu* gene in most varieties of modern corn is not promising as a wild plant. However, some

of the strains developed by combining pod corn with popcorn, especially those with tassel seeds, should be quite capable of perpetuating themselves in the wild in a suitable environment.

(F). The suggestion (30) that the characteristics of pod corn are the product of plant hormone action is quite valid but wholly irrelevant. It is undoubtedly true that pod corn involves plant hormone action, but we do not see how this fact can be regarded as evidence against the idea of pod corn as the ancestral form. We would assume that some of the principal changes which have occurred in the maize plant during the course of its evolution under domestication are concerned with the nature and amount of various plant hormones or in the manner in which these act. Indeed, we suspect that one of the effects of the pod-corn gene is to direct the plant's energy into terminal inflorescences and that one of the reasons why modern homozygous pod corn is usually monstrous is because all of the energy of a massive single stalk goes into a single terminal inflorescence. Our crosses of pod corn and popcorn indicate that terminal inflorescences are less monstrous when they occur on a plant with a number of stalks. A freely-tillering plant undoubtedly has a different hormonal complex than a single-stalked one.

(G). The conclusion that the half-tunicate form of pod corn, although in some respects more promising as a wild ancestor than the full tunicate, involves only the glumes of the ear, is erroneous and results from confusing half tunicate with the character, first recognized as "pallee sviluppate" by Bonvicini (3), later by Andres (2) as "semivestidos" and more recently by Galinat (10) as "papyrescent." Weatherwax's (30) illustration of half tunicate is almost certainly that of a papyrescent ear. Mangelsdorf (13) once made a similar error but was fortunate, as the result of test crosses, in discovering it be-

fore drawing conclusions about the nature of pod corn. The ear of Peruvian corn, which he illustrated (13) as a form of pod corn, proved upon further study, including its introduction into uniform inbred strains, to be not half tunicate but rather the character now known as papyrescent. This character does appear to affect only the glumes of the pistillate inflorescence and in this respect differs decidedly from half tunicate which, as will be shown by data presented later, produces virtually all of the effects of tunicate, only in a lesser degree.

We ourselves have given serious consideration to the possibility that half tunicate, rather than tunicate, is the ancestral type and that the latter may be an extreme form — the product of a pseudoallelic locus which has arisen during domestication as a mutation resulting from the duplication of an existing locus. We do not yet rule out this possibility; indeed we have for some years been developing stocks to determine whether the *Tu* locus is a compound one whose elements are sometimes separated by crossing over to produce “mutations” to half tunicate.

A preliminary experiment on this point conducted in the summer of 1958 produced one apparent mutation from tunicate to half tunicate which was accompanied by crossing over between the *su* and *gl₃* loci on chromosome 4.

But whether tunicate or half tunicate is the ancestral form is of secondary importance since both are pod corn and both involve the *Tu* locus on chromosome 4. There can be no doubt that there have been changes at this locus and little doubt that these changes have been a factor in corn's evolution under domestication. This is demonstrated by the facts set forth below.

THE EFFECTS OF THE ALLELES AT THE *Tu* LOCUS

One result of our intensive study of pod corn has been

the discovery of alleles, previously unknown, at the *Tu* locus, the most useful of which is the intermediate allele *tu^h*. By incorporating the two higher alleles in the series, *Tu* and *tu^h*, into a uniform inbred strain (A158) through repeated backcrossing, it has been possible to produce six distinct genotypes as follows: *TuTu*, *Tutu^h*, *Tutu*, *tu^htu^h*, *tu^htu*, *tutu*. A comparison in a large number of characteristics of these six genotypes has now been made and the data have been briefly summarized in a preliminary statement (16) and will be reported in detail elsewhere. It can be said here that a comparison of the six genotypes, which are isogenic except for the *Tu-tu* locus, provides a clearer understanding than we have had before of what these genes actually do. And what they do is both remarkable and highly significant with respect to gaining a conception of corn's evolution under domestication. Data on several of the characteristics which were studied are presented in TABLE I. They show that in proceeding through this series of six genotypes in the direction from *TuTu* to *tutu* the following changes occur: (a) A decline in the prominence of the terminal inflorescence, the tassel, and a corresponding increase in the development of the lateral inflorescence, the ear. (b) A change from a predominantly pistillate tassel to a wholly staminate one. (c) A progressive decrease in the length and weight of the glumes and a corresponding increase in the size and weight of the rachis.

All of these profound changes are of a kind which might have occurred in evolution under domestication; all of them tend to make the corn plant less able to survive in the wild and more useful to man. It is important to note, for example, that reduction in the weight of the tassel has been accompanied by an increase approximately five times as great in the weight of the ear, the food-storage organ. Likewise, the reduction in the pistillate

TABLE I. Six isogenic stocks, differing in alleles at the *Tu* locus, compared in various characteristics.

Characteristics	Genotypes					
	<i>TuTu</i>	<i>Tutu^h</i>	<i>Tutu</i>	<i>tu^htu^h</i>	<i>tu^htu</i>	<i>tutu</i>
Total weight inflorescences, gms.	28.9	39.9	72.2	98.9	133.3	130.1
Weight of tassels	28.9	18.3	12.7	9.2	6.7	4.9
Weight of ears	0.0	21.6	59.5	89.7	126.6	125.2
Percentage of total in ears	0.0	54.1	82.4	90.7	95.0	96.2
Percent pistillate spikelets in tassels	79.9	0.9	0.0	0.0	0.0	0.0
Average length staminate glumes, cms.	2.7	1.9	1.7	1.4	1.2	1.0
Total weight of cobs, gms.	0.0	6.4	20.6	24.5	24.0	22.7
Weight of pistillate glumes	0.0	5.3	16.5	17.7	14.2	8.7
Weight of rachises	0.0	1.1	4.1	6.8	10.5	10.9
Percentage of total in rachises	—	17.2	19.9	27.8	42.5	55.6

glumes, which are not needed in cultivated maize, has been accompanied by an increase in the size and weight of the rachis, which is both the grain-bearing structure and the container of the system of supply. In short, a substantial part of corn's evolution under domestication can be explained by a change in the hereditary material at this single locus. No such profound and significant changes in the direction away from a wild plant toward a highly useful, domesticated one can be demonstrated for teopod or corn grass or any other character in corn.

Perhaps it should be stated that we do not regard the monstrous pod corn represented by the genotype *TuTu* in this particular series as a model of the ancestral form. It probably does have some of the essential characteristics of wild corn—tassel seeds, long glumes, slender rachises—but in highly exaggerated forms. Consequently a comparison of the six genotypes on this particular genetic background provides a kind of biologically magnified view of some of the changes which have occurred in evolution under domestication.

THE EVIDENCE FROM PREHISTORIC CORN

If pod corn is the ancestral type, it should occur in some collections of prehistoric corn and possibly in representations on prehistoric pottery. It was while searching for such representations that we discovered in the Peabody Museum of Yale University a ceramic specimen which we described some years ago as possibly being pod corn (17). We also illustrated a second specimen from the same museum which might be so interpreted. Since then, we have seen ceramic replicas which might represent pod corn in the Museum of the University of Pennsylvania and in the Museum of the University of Cuzco in Peru. Two of the latter are illustrated by Weatherwax (30, Fig. 44).

Weatherwax (30) doubts that the Peabody Museum specimens represent pod corn and suggests that they are replicas or even casts³ made from nontunicate ears whose overlapping grains have long, attenuated tips. He illustrates such an ear (30) and suggests that it might have served as a model for the prehistoric ceramic specimens.

Weatherwax has overlooked an important difference between one of the ceramic replicas and the modern Peruvian ear with imbricated kernels—the variation in length of the individual units. The glumes of pod corn are usually longest at the base of the ear and become progressively shorter toward the tip. This is well illustrated in Weatherwax's Fig. 51 (lower center) which shows variation in the spikelets of a single ear of pod corn. This same kind of variation is exhibited in some degree in the units of the prehistoric ceramic replica but it is conspicuously absent in the kernels of the modern Peruvian ear (cf. Weatherwax, Fig. 51, upper left, center and right).

³ There is no possibility of making a realistic representation of overlapping kernels from the cast of an ear; each kernel must be fashioned separately and inserted in its proper place.

Consequently our original interpretation of the ceramic specimen as possibly representing pod corn still seems to us more plausible than Weatherwax's.

Weatherwax's suggestion is, however, quite useful in raising an entirely different question. Why are non-tunicate ears with pointed, imbricated kernels common in Peru and other countries of Latin America (6, 22, 32, 34) and why are they even more common in archaeological specimens and in prehistoric ceramic replicas (17, 30, 35, 36)?

One answer to this question—the correct one we suspect—is that pointed, imbricated kernels represent, as does pod corn, an ancient, relict, wild character which still persists in cultivated corn especially in certain Peruvian races. We know that kernels of modern pod corn are often pointed; they are squeezed into this shape during their development by the pressure of glumes. Indeed, when occurring in the tassels, if they fail to become pointed through pressure, they spread the glumes apart thus inviting the depredations of insects and birds. Such a characteristic would have a low survival value in nature. Consequently, we are forced to assume that, although the kernels of wild pod corn were pointed, this shape was determined in part genetically and not alone by pressure applied during development, as is also the case in the kernels of corn's relatives, *Tripsacum* and teosinte. When the tunicate character was lost through mutation the pointed, imbricated grains persisted for a time and are still found widely distributed in some varieties. They are, however, less common now than they were prehistorically and are probably destined to disappear completely, since they have no apparent survival value.

Here is an excellent example of the usefulness of controversy. By raising doubts about our conclusions on the

nature of prehistoric replicas of pod corn, Weatherwax has compelled us to examine the significance of pointed, imbricated kernels with the result that we have found a far more plausible explanation for their occurrence than that which we had earlier (17) proposed—the introgression of *Tripsacum* and teosinte.

More useful than ceramic replicas are actual prehistoric specimens. Mangelsdorf (13) pointed out that many prehistoric cobs have the deep pockets, with the general aspects of a honey comb, of heterozygous half tunicate and concluded that these represent a weak form of pod corn. Later, Mangelsdorf and Smith (19) found that many of the prehistoric cobs of Bat Cave have the long glumes and slender rachises characteristic of weak pod corn and concluded that these, like the Peruvian cobs, involve an expression of alleles at the *Tu* locus. Both Weatherwax (29) and Randolph (20) have expressed skepticism of the conclusion. Weatherwax's statement on this point follows:

The illustrations shown are not very convincing as to the tunicate character of the materials at any level, and there must be something wrong with the artist's reconstruction of the primitive podded ear, in which the *individual grains*, rather than the *pairs of grains*, seem to be spirally arranged.

The suspicion that "... there must be something wrong with the artist's reconstruction ..." is a classic example of an observation colored by inhospitality to an unwelcome idea. The fact is that the artist's reconstruction was printed side by side with an actual photograph of the prehistoric specimen which shows clearly that the individual spikelets are indeed spirally arranged. Nor is this an unusual pattern in prehistoric corn. It would be surprising if Weatherwax had not himself encountered it. Anderson (1) described some of the prehistoric Peruvian specimens as having cross spirals, like a pine cone.

It is unfortunate, we think, that Weatherwax's erroneous statement, which reflects upon the accuracy of the artist, has never been corrected, although there have been several opportunities in subsequent publications for doing so.

The basis for skepticism regarding the tunicate nature of other prehistoric specimens which we have described as weak forms of pod corn is little if any better. It is true that only a few prehistoric specimens resembling modern pod corn have been found (8, 11), but this is not, in any case, the kind of pod corn that we should expect to find commonly among prehistoric specimens. If modern pod corn is monstrous because it has lost its modifiers, then prehistoric pod corn, not so far removed from wild corn, should be a more restrained form. As mentioned above, Mangelsdorf (13) has shown that some of the prehistoric corn of Peru has glumes similar to those occurring in heterozygous, half-tunicate modern maize. More recently, we have discovered (15) in a variety of popcorn a major inhibitor of the tunicate character and it has been possible by combining this gene with the *Tu* and *tu^h* genes to synthesize a wide range of types matching many of the prehistoric specimens. We know of no other way in which such matching specimens can be synthesized.

The question of whether or not the prehistoric corn with relatively long glumes and slender rachises is pod corn finally becomes little more than an exercise in semantics. Randolph, for example, states (20):

It is difficult to see in these specimens of the most ancient cultivated maize thus far discovered, or in the existing wild relatives of maize, any support for the hypothesis that maize originated from a primitive type of pod corn of the sort that is known to be controlled by the dominant *Tu* allele in chromosome 4 of maize.

And Weatherwax, in commenting upon the possible

differences between modern cultivated corn and the original pod corn, states (30):

It may be contended that these deficiencies of pod corn are due to characteristics of cultivated corn which have been superimposed upon its original nature by recent hybridization, but there is a question as to how much liberty of this sort we may take with the plant and still call it pod corn or talk about its characteristics as being primitive.

It is true that when we proposed the pod-corn theory we had in mind a restrained form of pod corn controlled by the *Tu* gene on chromosome 4 in combination with a complex of modifying factors. Since then, as the result of intensive studies of pod corn, stimulated and guided by this part of our theory, we have discovered not only lower alleles at this locus but also modifying and inhibiting factors. Various combinations of these alleles and modifying and inhibiting factors can produce a gamut of types ranging from those in which the glumes are scarcely longer than those of modern varieties of sweet corn to those in which the glumes are several inches in length. In this wide range, where does normal corn end and pod corn begin? We have weak forms of the genotype *Tutu* whose glumes are much less conspicuous than those found in monstrous forms of the genotype *tu^htu^h*. Is one of these pod corn and the other not and which is the pod corn?

Until specimens matching prehistoric cobs are synthesized by methods other than the one which we have successfully employed—that of combining alleles at the *Tu* locus with inhibiting and modifying factors—we shall continue to assume that these prehistoric specimens possessing relatively long glumes and slender rachises are forms of pod corn.

POD CORN IN LIVING VARIETIES

The conclusion that changes at the *Tu* locus on chromosome 4 represent an important factor in the evolution

of maize under domestication is further supported by the occurrence—more widespread than had previously been suspected—of various forms of pod corn among the living varieties of this hemisphere. The extreme form conditioned by the *Tu* gene has been found in Colombia, Brazil, Peru and Bolivia. It is apparently quite common in Bolivia where, according to a report from Señor Dick Edgar Ibarra Grasso, Director, Museo Arqueológico, Universidad Mayor de San Simon, Cochabamba, Bolivia, it occurs in many of the valleys on the eastern slopes of the Andes.

The half-tunicate form of pod corn controlled by the *tu^h* locus has appeared in varieties from Ecuador, Paraguay and Peru (14). It, or something like it, is rather common in a Peruvian coastal race, Perla. Mr. Alexander Grobman of the National School of Agriculture near Lima has reported that one to two percent of the inbred strains isolated from this race are segregating for half-tunicate; in some collections the frequency is even higher.

How is this situation to be explained? Either wild corn was pod corn and had the genotype *TuTu* or *tu^htu^h* or it was not and had the genotype *tutu*. If it was not pod corn, then the *Tu* and *tu^h* genes now found in corn must represent mutations from the lower allele to the higher alleles in the series. Mutations from lower to higher alleles do occur but are not common. More difficult to explain is the preservation of these higher alleles if they are not the original ones. We can perhaps imagine that the pod corn controlled by the *Tu* allele was preserved by man as a curiosity or for its supposed magical properties, but this could scarcely be true of the weak pod corn controlled by the *tu^h* gene since in the heterozygous condition it is not generally recognized. Yet, because of competition between glumes and kernels, the weak pod corn undoubtedly causes some reduction in the yield of grain

and would be expected to have a low survival value. Why, then, should this allele have even a higher frequency than the *Tu* allele?

All of these difficulties can be avoided and the problem becomes quite simple if we assume instead that wild corn was *TuTu* which gave rise through mutations to the lower alleles, *tu^h* and *tu*. The *Tu* gene has largely disappeared; the *tu^h* gene is in the process of disappearing; and it would seem that eventually all of the world's corn will be *tutu*, the most efficient genotype from the standpoint of usefulness to man.

Another assumption mentioned earlier, which is almost equally simple and plausible, is that wild corn was half tunicate, *tu^htu^h*, which, through mutation, gave rise to the nontunicate genotype, *tutu*, and, through unequal crossing over, to the strongly tunicate form *TuTu*. The first might have been preserved because of its obvious usefulness, the second because of its supposed magical properties.

It should be noted that both of the above assumptions postulate that the progenitor of cultivated corn was a form of pod corn and that changes at the *Tu-tu* locus have been involved in corn's evolution under domestication.

RECONSTRUCTING THE ANCESTOR OF CORN

Perhaps the strongest support for the pod-corn theory is provided by a genetic reconstruction of the ancestral form (15). This was accomplished by crossing pod corn with a number of freely-tillering varieties of popcorn and through selection combining the *Tu* gene with a complex of minus modifying factors and a majoring inhibiting factor. The plants so produced have several stalks; the tassels bear both male and female flowers, the former above and the latter below on the same branches; the

branches are brittle when mature, breaking apart easily when disturbed by the wind or by birds, thus providing a mechanism for the dispersal of the seeds. When ears occur, they are borne at high positions on the stalk. In these positions, the ears are small, sometimes branched, bear both male and female flowers, and are enclosed by only a few husks which flare open at maturity, allowing the fragile ear to disperse its glume-covered seeds. Plants of this reconstructed ancestral form have many of the characteristics of a good wild grass, and they show a striking similarity in several of their botanical characteristics to *Tripsacum*, a wild relative of maize. As mentioned above, this reconstructed form, with some additional modifications brought about by selection, might survive in nature in a suitable environment.

This true-breeding pod corn shows a resemblance in its principal botanical characteristics to Weatherwax's hypothetical ancestor of the American *Maydeae* which he described as follows (29):

We picture the ancestral form as a plant with the habit of teosinte or of some of the tropical species of *Tripsacum*, with paniculate inflorescence terminating the main culm and the branches. Each inflorescence had pairs of staminate spikelets in the terminal portion and pairs of pistillate spikelets toward the base of each of its branches. The staminate spikelet was two-flowered, but the pistillate had only one functional flower and a rudiment of another. The lower glume of the pistillate spikelet and the adjacent rachis segment had probably not yet developed into a hard shell.

Except that it is an annual and often has both male and female spikelets in both inflorescences, the reconstructed form is similar to the hypothetical wild maize with which domestication began, described by Weatherwax as follows (29):

It is conceivable, however, that there came a time when, by natural processes, it had taken on an appearance not very different from that of some relatively undeveloped varieties cultivated today. That is, it had terminal staminate panicles on a few main culms and pistillate

panicles in various stages of reduction to the spicate form on numerous branches. The small ears, with eight or more rows of grain, were partly enclosed in the leaf sheaths, and the small grains were partly enclosed in the bracts of the spikelets.

How are we to account for the close resemblance between Weatherwax's hypothetical and our genetically reconstructed ancestral form? Weatherwax has assumed that the nature of corn's progenitor could be deduced from a study of the characteristics of its living descendants and relatives. We have assumed that genes controlling the principal characteristics of wild corn are not likely to have been completely lost in several thousand generations of domestication; that they still exist in cultivated varieties; and that the ancestral form can be reconstructed by recombining them. The fact that the two methods produce essentially the same end result is either a remarkable coincidence or an indication that both methods are valid and that the picture of corn's ancestor which both produce may be a reasonably accurate one.

SUMMARY

The evidence for and against the pod-corn theory has been reviewed; the principal objections to it have been considered; and plausible answers to all of them have been found in the evidence now at hand.

1. Pod corn is "equivocal" only when its genetic background is variable. In inbred strains or in uniform F_1 hybrids the pod character is no more variable than other characteristics of the plant.

2. Modern pod corn is often monstrous and sometimes sterile because it is the product of an ancient relict gene superimposed upon highly heterozygous, vigorous modern varieties. It is neither monstrous nor sterile when combined with other primitive characters.

3. Pod corn differs from other monstrous forms such as teopod and corn grass in always exhibiting one characteristic which wild corn must have had: kernels enclosed and protected by glumes.

4. When pod corn is combined with some of the genes of certain varieties of popcorn it exhibits a number of characters of a wild grass: a freely-branching growth habit, small pointed seeds, glumes enclosing the seeds and a means of seed dispersal.

5. The fact that pod corn may be the product of plant hormone action does not rule it out as the ancestral form. Changes in plant hormone systems are to be expected during evolution under domestication.

6. Although modern monstrous pod corn could not exist in the wild, some of the forms produced by crossing popcorn and pod corn are probably capable of doing so in a suitable environment.

7. The conclusion that the half-tunicate form of pod corn could not be the ancestral type because it involves only the glumes is a result of confusing this characteristic with another, the papyrescent.

8. The fact that pointed, imbricated kernels have a higher frequency in prehistoric corn than in modern corn suggests that they represent a primitive character once associated with the podded condition.

9. Prehistoric cobs suspected of representing various types of pod corn can be matched by combining the alleles of the *Tu* locus with various modifying and inhibiting genes.

10. One of the lower alleles of pod corn, *tu^h*, has a high frequency in living varieties. This would not be expected if wild corn had been of the genotype *tutu* and if *tu^h* represents a mutation occurring during domestication.

11. A genetically reconstructed ancestral form produced by combining the characteristics of pod corn with those of certain varieties of popcorn is identical in virtually all of its characteristics with the hypothetical ancestral form, based upon comparative morphology, described by Weatherwax.

12. It is concluded that the pod-corn theory now has greater validity and more evidence in its support than when it was first proposed.

LITERATURE CITED

1. Anderson, E., 1947. Corn before Columbus. Pioneer Hi-Bred Corn Co. Des Moines.
2. Andres, J. M., 1950. Granos semivestidos, restos de un carácter ancestral del maiz. *Revista Argentina Agron.* 17: 252-256.
3. Bonvicini, M., 1932. Sulla eraditarietà di una anomalia nel mais. *L'Italia Agricola* 69: 3-9.
4. Brieger, F. G., 1943. Origem do milho. *Revista de Agric.* 18: 409-418.
5. —, 1944. Estudos experimentais sobre a origem do milho. *Anais Escola Superior Agric.* "Luiz de Queiroz" Seperata No. 10: 226-278.
6. —, 1945. Estudos genéticos sobre o milho tunicata. *Anais Escola Superior Agric.* "Luiz de Queiroz" Seperata No. 17: 209-238.
7. —, 1945. Estudos sobre a inflorescência de milho com referência especial aos problemas filogenéticos. *Bragantia* 5: 659-716.
8. Cutler, H. C., 1944. Medicine men and the preservation of a relict gene in maize. *Jour. Hered.* 25: 290-294.
9. Galinat, Walton C., 1954. Corn grass II. Effect of the corn grass gene on the development of the maize inflorescence. *Amer. Jour. Bot.* 41: 803-806.
10. —, 1957. The effects of certain genes on the outer pistillate glume of maize. *Bot. Mus. Leaflet. Harvard Univ.* 18: 57-76.
11. —, P. C. Mangelsdorf and L. Pierson, 1956. Estimates of teosinte introgression in archaeological maize. *Bot. Mus. Leaflet. Harvard Univ.* 17: 101-124.
12. Mangelsdorf, P. C., 1947. The origin and evolution of maize. *Advances in Genetics* 1: 161-207.
13. —, 1948. The role of pod corn in the origin and evolution of maize. *Ann. Missouri Bot. Gard.* 35: 377-406.

14. —, 1957. Half-tunicate from Peru, Ecuador and Paraguay. *Maize Gen. Coöp. News Letter* 31: 64.
15. —, 1958. Reconstructing the ancestor of corn. *Proc. Amer. Philos. Soc.* 102: 454-463.
16. — and Helen P., 1957. Genotypes involving the *Tu-tu* locus compared in isogenic stocks. *Maize Gen. Coöp. News Letter* 31: 65-66.
17. — and R. G. Reeves, 1939. The origin of Indian corn and its relatives. *Texas Agric. Exp. Sta. Bull.* 574.
18. — and R. G. Reeves, 1945. The origin of maize: present status of the problem. *Amer. Anthropologist* 47: 235-243.
19. — and C. E. Smith, Jr., 1949. New archaeological evidence on evolution in maize. *Bot. Mus. Leafl. Harvard Univ.* 13: 213-247.
20. Randolph, L. F., 1952. New evidence on the origin of maize. *Amer. Nat.* 86: 193-202.
21. Reeves, R. G., 1950. The use of teosinte in the improvement of corn inbreds. *Agron. Jour.* 42: 248-251.
22. Roberts, L. M., U. J. Grant, R. Ramirez E., W. H. Hatheway and D. L. Smith, *in collaboration with* P. C. Mangelsdorf, 1957. Races of maize of Colombia. *Nat. Acad. Sci.—Nat. Res. Council Publ. No.* 510.
23. Saint-Hilaire, A. de, 1829. Lettre sur une variété remarquable de maïs du Brésil. *Ann. Sci. Nat.* 16: 143-145.
24. Singleton, W. R., 1951. Inheritance of corn grass a macromutation in maize, and its possible significance as an ancestral type. *Amer. Nat.* 85: 81-96.
25. Sprague, G. F., 1955. *Corn and corn improvement.* New York, Academic Press.
26. Vachhani, M. V., 1950. A study of the relationship of chromosome knobs with certain agronomic and morphological characters in corn inbreds. *Agron. Jour.* 42: 196-201.
27. Weatherwax, P., 1923. *The story of the maize plant.* Univ. Chicago Press.
28. —, 1929. The morphological nature of teopod corn. *Jour. Hered.* 20: 325-330.

29. —, 1950. The history of corn. *Sci. Month.* 71: 50-60.
30. —, 1954. Indian corn in old America. New York, Macmillan.
31. —, 1955. History and origin of corn I. Early history of corn and theories as to its origin. *In* Corn and corn improvement: 1-16. New York, Academic Press.
32. Wellhausen, E. J., A. Fuentes O. and A. Hernandez C., *in collaboration with* P. C. Mangelsdorf, 1957. Races of maize in Central America. *Nat. Acad. Sci.-Nat. Res. Council Publ.* No. 511.
33. — and C. Prywer, 1954. Relationship between chromosome knob number and yield in corn. *Agron. Jour.* 46: 507-511.
34. —, L. M. Roberts and E. Hernandez X., *in collaboration with* P. C. Mangelsdorf, 1952. Races of maize in Mexico. *Bussey Inst. Harvard Univ.*
35. Wittmack, L., 1880. Ueber antiken Mais aus Nord-und Südamerika. *Zeitschrift f. Ethnologie* 12: 85-97.
36. —. Plants and fruits. *In* Reiss and Stübel, *The Necropolis of Ancon in Peru*. Vol. III, Part XIII. London and Berlin. 1880-1887.

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